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Population Biology of the Japanese Little-neck Clam, *Tapes philippinarum*, in Kaneohe Bay, Oahu, Hawaiian Islands[1]

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ABSTRACT: The Japanese little-neck clam, *Tapes philippinarum*, an introduced species in Kaneohe Bay, Oahu, Hawaiian Islands, has a thriving population only in a 1.35-hectare mud flat after heavy fishing triggered depletion in six other beds within the bay. Monthly gonad examination of the clams suggested that spawning occurs at a low level throughout the year with a peak from January to February. This observation is corroborated by the appearance of new recruits in the monthly sample from April to June and by their presence at low levels at other times of the year. Size-specific fecundity, determined indirectly from differences in the length: dry weight relationships of ripe and spent clams, ranges from 432,000 eggs in a 20-mm clam, increasing exponentially to 1.35×10^6 eggs in a 40-mm clam.

Estimates of the population of clams 11 mm and larger, which were 3.09×10^6 in 1970 and 3.4×10^6 in 1972, show a growth of 5 percent per year during the 2-year period; monthly quantitative sampling showed no evidence of population growth after 1972. A survivorship curve obtained from the monthly samples gave a total instantaneous mortality of $z = 0.2005$. The age-specific mortality agrees with the age-frequency of the empty shells collected from the bed, with a correlation coefficient of 0.9345 with 4 d.f. The condition of the empty shells indicated that 57 percent of the mortality is attributable to crab predation, mainly by *Thalamita crenata*, which constitutes 70 percent of the experimental crab catch in the clam bed. Sixty percent of the broken shells were 19.5 to 30.4 mm in length; in experiments with predation by *T. crenata*, 96 percent of those eaten fell within the 14.5 to 30.4 mm size range. The difference between the lower limits of the size ranges can be attributed to the size structure of the clams during the survey period. The experimental population had an artificially maintained size structure. Experimental exclusion of predators over a limited area suggested that crab predation regulates clam size structure but not clam density.

THE JAPANESE LITTLE-NECK CLAM, *Tapes philippinarum* Adams & Reeve, 1867, was introduced on Oahu from Japan in 1920. The original stock, 10 barrels of the clams, was planted in Kalihi Basin, Pearl Harbor, and Kaneohe Bay, and the animals grew well in all localities except Kaneohe Bay (Edmondson and Wilson 1939). The clams have since disappeared from both Pearl Harbor and Kalihi Basin but have become established in Kaneohe Bay where an extensive population has been recognized by the Hawaii State Department of Land and National Resources (1964–1966, 1967–1968), Division of Fish and Game (1968). Beds of the clam were opened for harvesting in 1965. The major beds occurred on mud flats along the southeastern shore of Kaneohe Bay, with other small patches elsewhere. Higgins (1969)

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reported seven beds in 1967 and 1968; now only a single bed has a thriving population.

It has been suggested that an excess of fishing in Kaneohe Bay during a succession of open seasons between 1965 and 1968 triggered the clam's decline. The Hawaii State Division of Fish and Game reported 10,000 clam diggers in the 1965 season and 41,000 in 1967. The single remaining bed was officially closed to harvest in 1969 and has since remained closed. This bed was studied to determine whether the clam population is declining or recovering and to assess the amount of predation by crabs and their role as a potential regulatory factor in the maintenance of the clam populations.

Total Population Surveys

This study was conducted on a 1.35-hectare mud flat at the mouth of Kaneohe Stream (Figure 1). Total population surveys were made on two occasions: June 1970 (Murphy, unpublished) when two transect lines (X and Y, Figure 2) were used, and May 1972 when four transect lines (A, B, C, and X, Figure 2) were used. The orientation of the main transect lines was shifted during the 1972 survey on the basis of the density gradient revealed by the 1970 survey. Transect X was resampled for purposes of comparison.

On both surveys, pairs of 15 × 15 cm quadrats were taken along the transects at distances ranging from 1 to 10 meters, the distance depending on the abundance and change in the surface characteristics of the substrate. In the 1972 survey, the surface characteristics were carefully noted at each sampling point. In addition, seven substrate samples of 1000 cm^3 each, dug to a depth of 10 cm, were collected along transect X and subjected to particle size analysis using standard wet-sieving techniques.

Monthly Sampling

From March 1970 to December 1973, a monthly sample of approximately 300 clams was collected haphazardly with a shovel and 5.5-mm-mesh sieve within a 100 m^2 area. These samples provided the length-frequency data.

From March 1972 to December 1973, quantitative samples were collected with a 15 cm^2 quadrat box from five stations set 20 meters apart along transect A. Counts and measurements were made of individuals over 3 mm. The 1.98-mm-mesh sieve used did not effectively retain clams less than 3 mm.

Gonad Examination and Fecundity

From June 1971 to December 1973, a subsample of 40 to 50 clams from the monthly sample of 300 was opened and the gonad condition noted. Clams with flaccid gonads were considered spent. Turgid gonads were considered to be an indication of ripeness.

The gonads could not be excised free from other tissues, so I was unable to estimate fecundity by the methods usually used. All fecundity determinations on bivalves to date consist of inducing the animals to spawn in a known volume of water and subsequently estimating the total number of eggs discharged by using aliquot counts (Galtsoff 1930, Davis and Chanley 1956, Ansell 1967). This method is laborious and subject to chance. Some individual bivalves will not spawn even after repeated stimulation. *Tapes philippinarum* could not be stimulated to spawn even under conditions of temperature rise and gonadal suspension.

The observation that the length:dry weight relationship of spent and ripe *Tapes* varies significantly suggested an indirect method of fecundity determination. Like the length:weight data of most other organisms, those of *Tapes* fit the exponential relation $y = Ax^B$, where y = weight and x = length. The fit is equally good for both live and dry weight. Knowing the constants A and B for both spent and ripe clams, we can predict the dry weight of any size clam under both reproductive conditions. By taking the difference in the predicted dry weights between ripe and spent clams of the same length at various size points, we can then obtain a length:dry weight difference relationship.

If the weight difference is due solely to the loss of gonadal material, then the length:dry

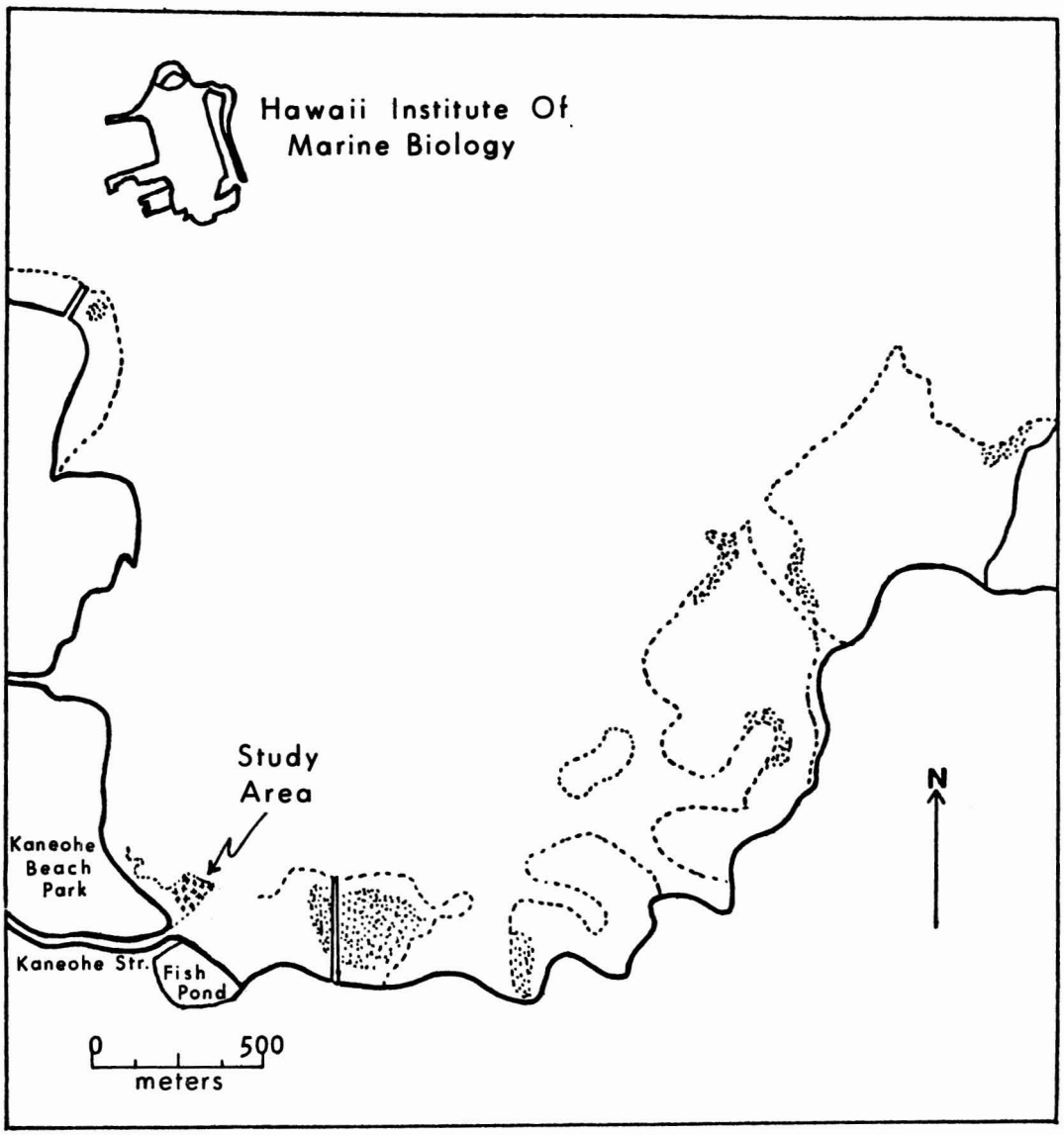


FIGURE 1. Southeastern portion of Kaneohe Bay, showing the location of the study area. Stippled areas are depleted beds.

weight difference relationship can be considered as a length:dry gonad weight relationship. The only datum needed to obtain size-specific fecundity is number of eggs per unit dry weight of gonadal material. I obtained this conversion factor empirically by stripping female clams of 0.1 ml of gonad material, using a glass pipette. Whenever the pipette clogged or an air bubble formed, I discarded the sample. Ten good samples were obtained in this manner from ten female clams ranging in size from 26.4 to 35.0 mm.

The gonad material so obtained was diluted with seawater to make 1 ml and was then split into two equal portions. One half was placed in tared and numbered aluminum

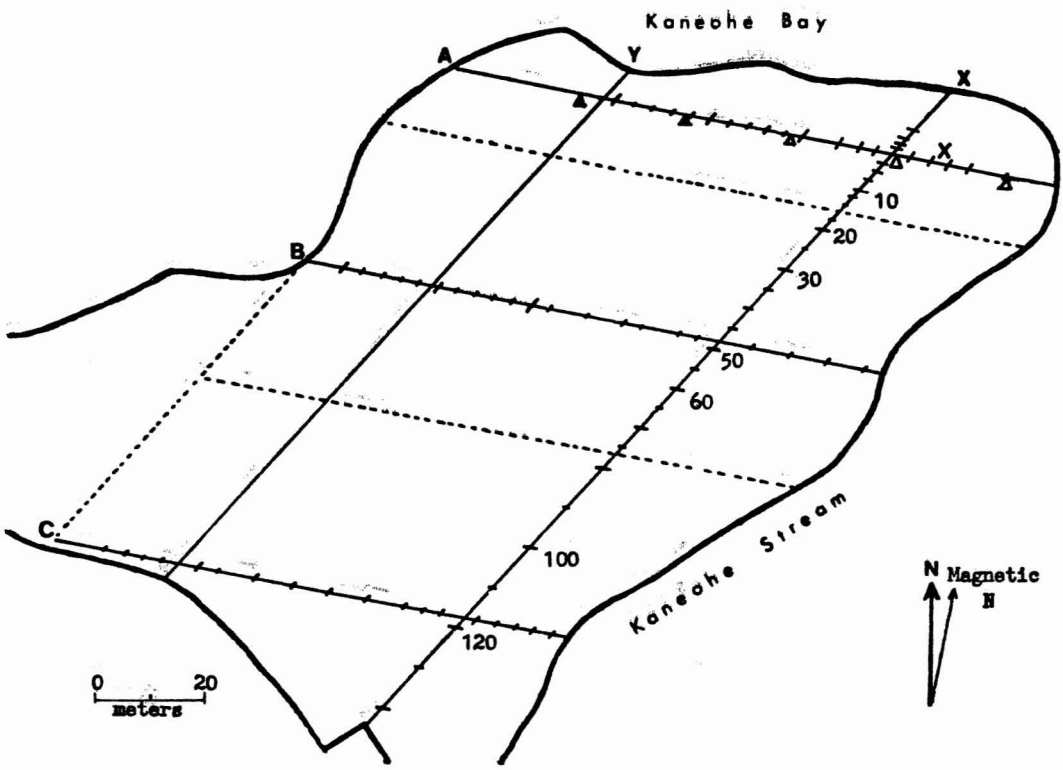


FIGURE 2. The study area, showing positions of transect lines and sampling points. Dotted lines divide the study area into three subareas representing three levels of density for computation purposes. Triangles, monthly sampling stations; numbered points, sampling points for substrate analysis.

foil pans and dried to constant weight at 60° C. The other half was diluted further to 10 ml and stirred; a hemacytometer was then used to make duplicate counts of the eggs in the suspension. Mean egg counts divided by mean dry weight provided the conversion factor necessary to obtain the size-specific fecundity.

Mortality Studies

I converted the length-frequencies from the monthly quantitative samples to age-frequencies using the von Bertalanffy growth parameters (Fabens 1965) calculated from the 1972 data. The resulting age-frequencies were standardized to number per age group per 0.25 m^2. A 2-month age interval was used to obtain a smooth distribution. The number of survivors in the April, May, and June 1972 cohorts were followed at 2-month intervals; this allowed an estimation of mortality rate. The data were grouped into odd and even months to facilitate computation.

An assessment was made of the empty shells in the clam bed. One sample of 167 empty shells was collected on 5 February 1973 over a 200 m^2 area. Collection was limited to shells meeting the following criteria: (1) lying on the surface; (2) hinges intact even if both valves were broken; (3) not covered by algal growth, i.e., did not have a greenish hue; and (4) nacre still fairly glossy. These criteria were set to limit collection to clams that had died at approximately the same period of time.

The empty shells were sorted according to the following conditions: (1) intact; (2) one or both valves chipped or broken; (3) one or both valves with hole present. These shells were measured and in cases where both valves were broken the size of the umbo was

TABLE 1

PARTICLE SIZE ANALYSES OF SUBSTRATE SAMPLES COLLECTED AT DIFFERENT LEVELS ALONG TRANSECT *X*; GRAIN SIZE SCALE FROM FALK (1965)

PARTICLE SIZE (mm)		PERCENT COMPOSITION BY WEIGHT AT STATION						
		10	20	30	50	60	100	120
Pebble,	4–64	20.6	50.1	46.3	40.9	15.0	40.4	54.2
Granule,	2–3.9	6.0	6.0	4.1	4.8	6.7	5.8	13.2
Coarse sand,	0.5–1.9	29.3	19.4	17.2	24.2	33.1	28.7	6.5
Medium sand,	0.25–0.49	25.8	11.5	15.8	11.6	13.8	13.3	10.0
Fine sand,	0.0625–0.24	14.1	8.7	10.8	13.0	15.8	6.5	9.4
Mud,	<0.0625	1.2	2.1	3.6	4.0	13.0	5.0	5.9
(Shells)		3.0	2.1	2.3	1.6	2.5	0.2	0.7

compared with that of an intact valve to give an estimate of the length.

Experiments on Predation

Laboratory experiments were conducted to determine clam size-specificity of predation by crabs. The experiments were carried out on a water table with each of five 0.186 m^2 compartments of the table divided into two equal parts with a 10-cm-deep wooden divider. One side was filled with substrate that had been collected from the clam bed and cleared of clams. Seawater was allowed to flow. Water depth over the substrate was about 10 cm. In each test the clams were allowed to bury themselves before the crabs were introduced.

In the test for size-specificity, two large male and one small female *Thalamita crenata* and two *Calappa calappa* were used. In all cases the experiments were terminated after 8 days.

An experiment was also conducted on the clam bed to determine the effect of predation on clam density and size structure. In each of the five sampling stations, a patch measuring 0.186 m^2 (2 × 2 ft) was covered with a sheet of galvanized wire screen having a mesh of 5.5 mm. A fold of 5 cm made on all four sides of the screen was buried so that a barrier was formed on the four sides and the screen was flush against the surface of the clam bed. The screens were anchored on all four corners by steel rods bent into a U with at least one leg 25 cm long. To prevent human interference, I coated the screens with coal tar to decrease their visibility; in spite of this, only one screen was left at the end of the year-long experimental period. After 1 year this screen was removed and a 25 × 25 cm quadrat was collected from within the protected area. A similar sample was also collected from a contiguous unprotected area which served as the control.

Crab species composition was obtained by setting ten lift nets 5 meters apart along transect *A*; shark meat and tuna head were used as bait. The duration of each set was from 30 to 45 minutes.

RESULTS

The Study Area

The substrate consisted of gravel, sand, and mud in proportions that varied with location, as shown in Table 1. Salinity measurements made with a refractometer indicated that the outflow from Kaneohe Stream does not substantially affect the salinity of the surface water over the bed except immediately after a rainfall (Table 2).

Of the epifauna of the clam bed, only the crabs were positively identified and counted. Oysters and barnacles in the area were relatively sparse because these animals require large objects for attachment.

The infauna consisted of polychaetes, two gastropod species, and a tellinid. The tellinid, *Quidnipagus palatam*, was common but not abundant. The gastropods *Polinices* sp. and *Natica* sp. were extremely rare. In 11 monthly

TABLE 2

SALINITY OF SURFACE WATER OVER CLAM BED TAKEN ALONG A LINE PERPENDICULAR TO KANEOHE STREAM

SAMPLING TIME	BAY WATER	DISTANCE FROM KANEOHE STREAM (meters) 0	40	80
After heavy rainfall				
25 January 1971	32.5	10.0	18.0	30.0
25 February 1972	31.0	8.0	22.0	28.0
15 May 1972	32.0	10.0	25.0	27.0
No rainfall				
17 March 1972	32.0	20.0	32.0	31.0
11 July 1972	33.0	24.0	30.5	31.0

TABLE 3

OCCURRENCE OF *Tapes philippinarum* AND OTHER MOLLUSKS IN 210 QUADRATS (15 × 15 cm) COLLECTED 18–31 MAY 1972

	Tapes	TELLINID	GASTROPODS
Number of positive quadrats	206	70	5
Occurrence, %	98.1	33.3	2.4
Average number per positive quadrat	19.4	1.7	1.0
Range	1–69	1–6	1

TABLE 4

CALCULATION FOR TOTAL POPULATION ESTIMATE BASED UPON POPULATION SURVEY OF 12–31 MAY 1972; STRATIFIED SAMPLING METHOD AND NOTATION FROM COCHRAN (1963); TRANSECT *X* SAMPLES POOLED WITH SUBAREAS *A*, *B*, OR *C*, DEPENDING UPON LOCATION

	SUBAREAS *A*	*B*	*C*
N_h	115,556	262,222	222,222
N		(600,000)	
n_h	78	76	56
n		(210)	
$\bar{Y}_h \sim \bar{y}_h$	30.26	16.75	6.75
$\bar{Y} \sim \bar{y}_{st}$		(15.65)	
W_h	0.193	0.437	0.370
s_n	14.80	12.07	5.42
$s(\bar{y}_{st})^2$		(0.564)	
d.f.		(207)	

Population mean	15.65 ± 1.48 per quadrat
Population total	
>3 mm	9,390,000 ± 888,000
>11 mm	3,400,000 ± 321,278
1970 estimate	
>11 mm	3,090,000

NOTE: N_h = number of possible sampling units per subarea
N = total number of possible sampling units
n_h = number of units sampled per subarea
n = total number of units sampled
$\bar{Y}_h$ = sample mean; estimate of $\bar{Y}_h$, the true mean
$\bar{Y}_{st}$ = estimate of $\bar{Y}$, the population mean per unit
W_h = relative weight per subarea
s_n = sample variance
$s(\bar{y}_{st})^2$ = variance

samples collected in 1972, the tellinid was encountered seven times and the gastropods twice. Table 3 shows the abundance of other mollusks relative to *Tapes philippinarum*. The polychaetes were found in each month's sample, but no attempt was made to count them because they were extremely difficult to extricate intact from the 5.5-mm-mesh sieve that was used.

The crabs were the most important organisms in the clam bed relative to the clams. They are discussed in the section on predation.

The counts of clams show a gradation in density along transect *X*. For this reason I decided, for computation of the total population size, to divide the clam bed into three sectors based upon the density gradient along transect *X*, with the high-density sector being represented by transect *A*, the medium-density by transect *B*, and the low-density by transect *C* (Figure 3).

The total population of clams 3 mm and larger (that portion effectively retained by smallest sieve used—1.98 mm) was estimated, with the calculations for stratified samples (Cochran 1963) and for area-density method (Rounsefell and Everhart 1953) being used to make the estimate. Although both methods of calculation are considered valid only for random samples, practical considerations of time involved, extent of area sampled, and accuracy in pinpointing sampling points with the use of transects probably outweigh the added accuracy to be gained by random sampling. The stratified technique gave a total population estimate of $9.39 \times 10^6 \pm 888{,}000$ clams 3 mm and larger (see Table 4). The area-density method gave an estimate of 9.14×10^6, a difference of only 2.74 percent.

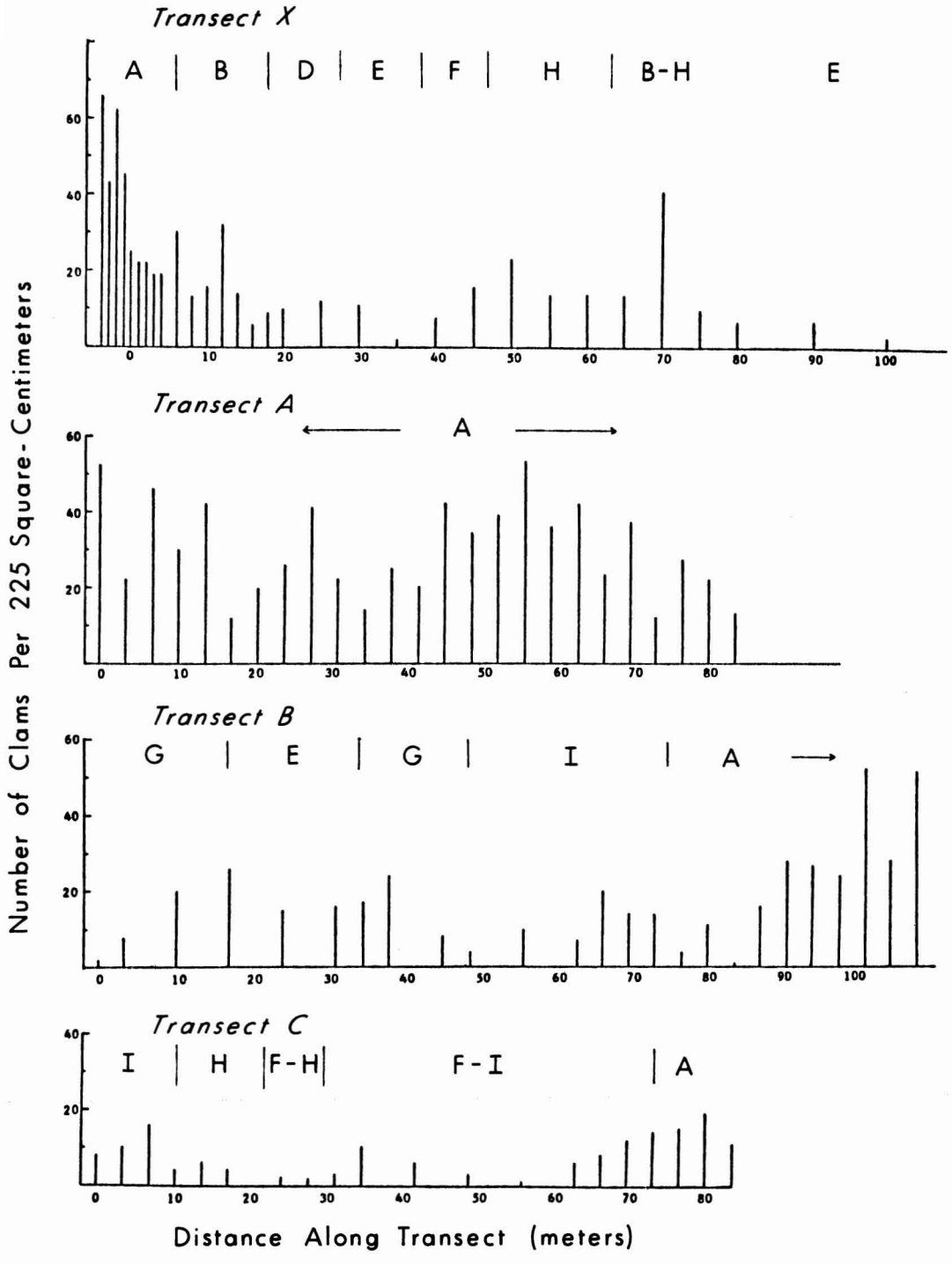
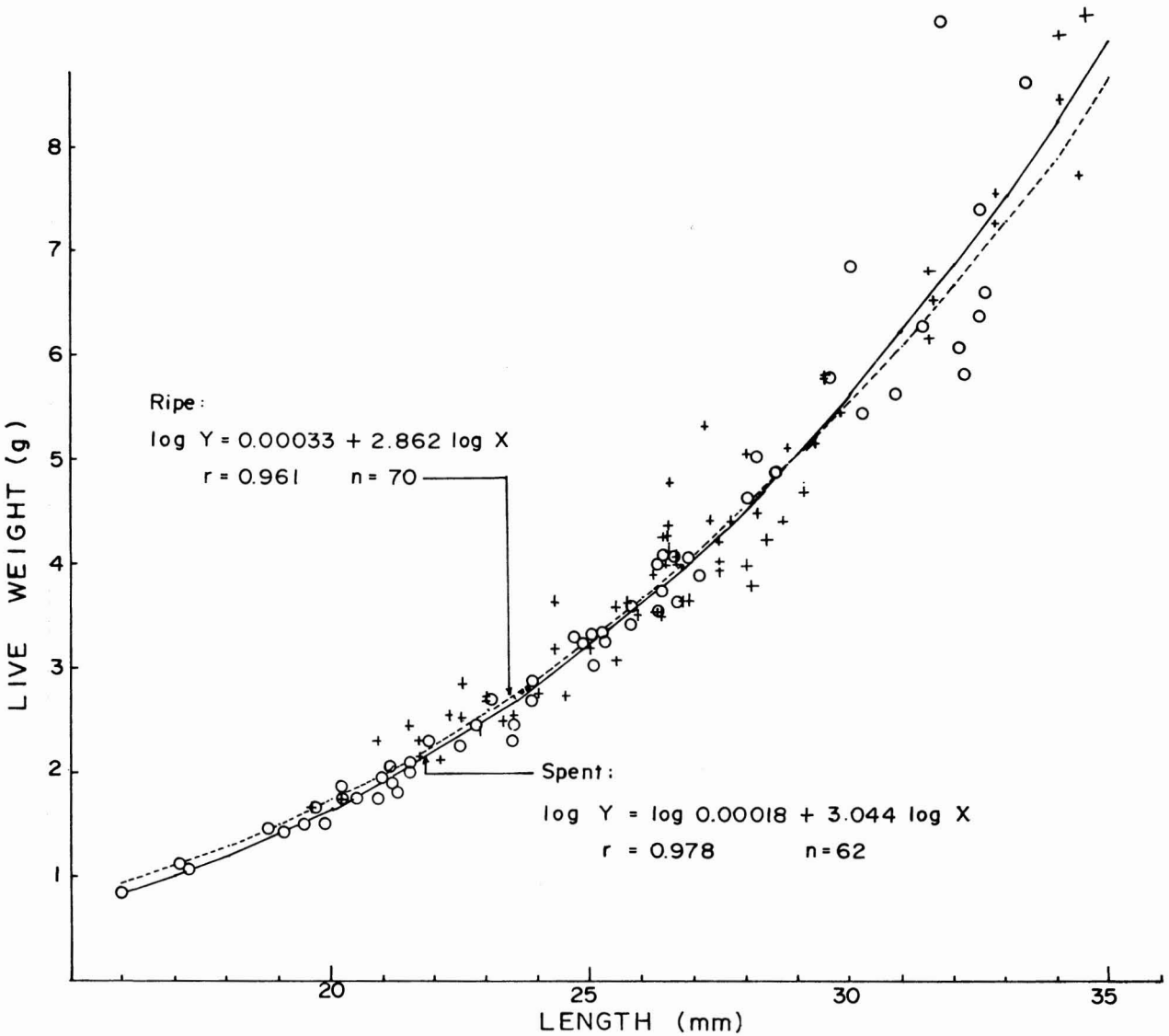


FIGURE 3. Density of *Tapes philippinarum* and substrate characteristics along the four transects sampled from 12–31 May 1972. *A*, pebble; *B*, sparse pebble; *C*, dense pebble; *D*, cobble; *E*, cobble, small boulders; *F*, sparse cobble; *G*, dense cobble; *H*, sandy; *I*, sandy mud.


LIVE WEIGHT (g)
LENGTH (mm)
Ripe:
log Y = 0.00033 + 2.862 log X
r = 0.961 n = 70
Spent:
log Y = log 0.00018 + 3.044 log X
r = 0.978 n = 62

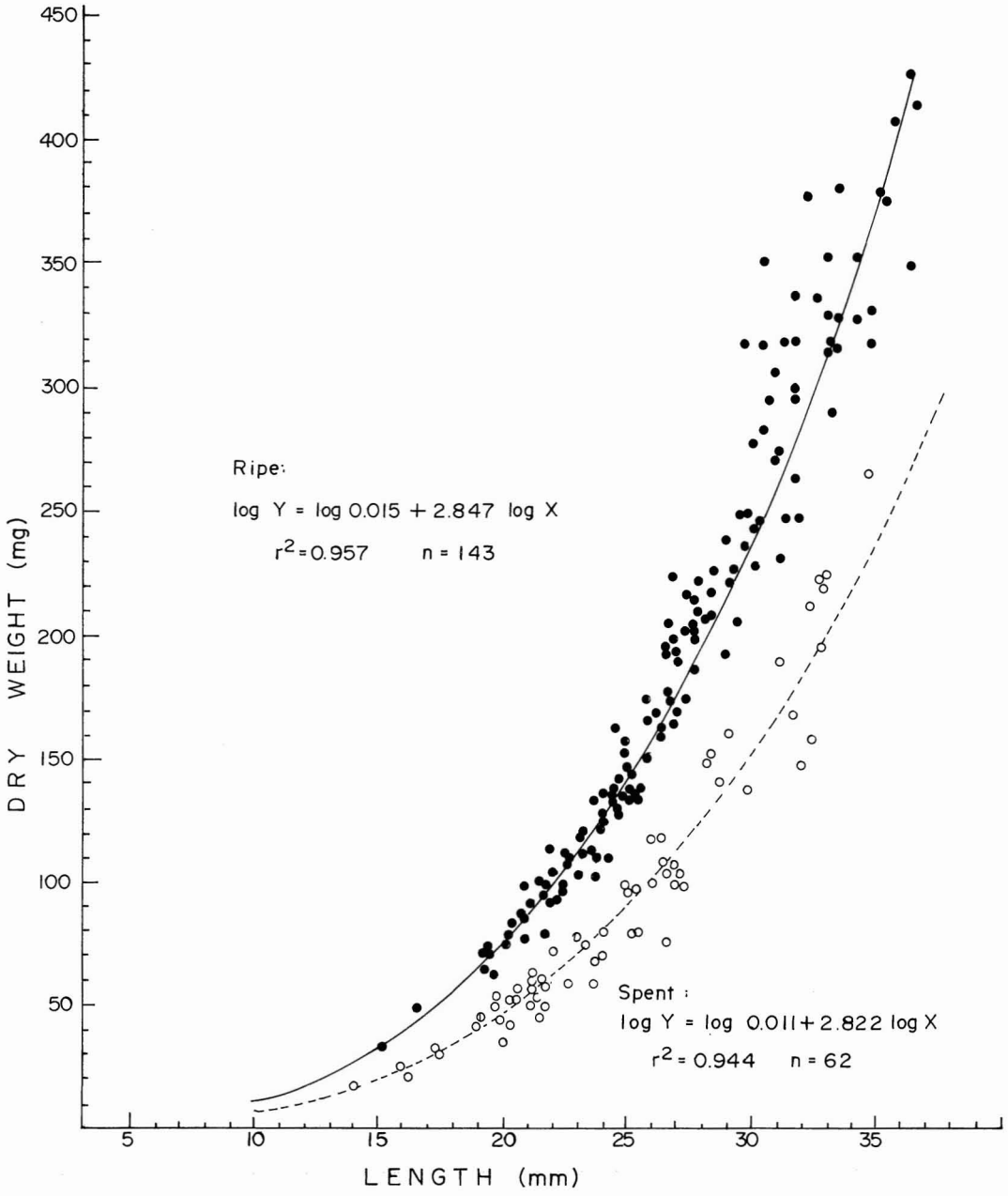


FIGURE 5. Length : dry weight relationship of *Tapes philippinarum*, ripe (crosses) and spent (open circles).

Length : Weight Relationships

Periodic weighing showed no variation with time in the length : live weight relationship (Figure 4). However, the variation was marked in the length : dry weight relationship (Figure 5). A two-tailed *F*-test of the mean squares of the length : dry weight regression shows a significant difference in the elevations between the February sample (spent) and

TABLE 5

COMPARISON OF REGRESSION LINES; LENGTH : DRY WEIGHT RELATIONSHIP; SPENT AND RIPE FEMALE, RIPE MALE AND RIPE FEMALE

SOURCE	DEVIATIONS FROM REGRESSION d.f.	MEAN SQUARE
Within		
Spent	60	0.01764
Ripe ♀	68	0.00876
Ripe ♂	71	0.00868
Spent and ripe ♀	128	0.01292
Ripe ♀ and ripe ♂	139	0.00872
Pooled		
Spent and ripe ♀	129	0.01289
Ripe ♀ and ripe ♂	140	0.00867
Difference between slopes		
Spent and ripe ♀	1	0.00870
Ripe ♀ and ripe ♂	1	0.00230
Between adjusted means		
Spent and ripe ♀	1	7.36975
Ripe ♀ and ripe ♂	1	0.00721

F VALUES	VARIANCES	SLOPES	ELEVATIONS
Spent and ripe ♀	2.013*	0.67337	571.74166†
Ripe ♀ and ripe ♂	1.0092	0.26376	0.83160

*Significant at $P = 0.01$ level.
†Significant at $P = 0.001$ level.

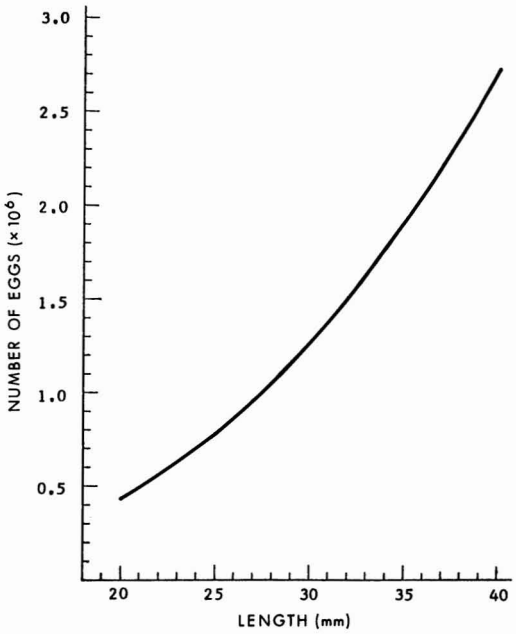


FIGURE 6. Fecundity of *Tapes philippinarum*; data based upon dry weight differences between ripe and spent clams.

the June sample (ripe). The spent clams could not be sexed but, because I found no difference between ripe males and females in length : dry weight relationship, I compared the spent clams only with the ripe females as I was interested only in female fecundity (Table 5). The significant difference in elevations between ripe and spent clams is the basis of the indirect method of determining size-specific fecundity as detailed earlier.

Size at First Maturity

Of the more than 2000 clams examined during the monthly gonad examinations, only one 15.1-mm individual contained sperm cells and one 15.3-mm individual contained egg cells. As a general rule, however, the gonads were poorly developed in clams under 20 mm in length, an observation consonant with that of Higgins (1969). Therefore, the spawning stock was believed to consist of individuals above 20 mm in length.

The fecundity of *Tapes philippinarum* ranges from 432,000 eggs in a 20-mm clam and increases exponentially to 2.35×10^6 eggs in a 40-mm clam (Figure 6). Egg counts made on three ripe clams, 25.0, 30.0, 35.0 mm in length and stripped of all their gonad material as thoroughly as possible, fell within the expected limits of the indirectly obtained fecundity curve.

Spawning Season and Frequency

The condition of the gonads indicated that spawning occurs throughout the year, peaking from December to February. This observation is corroborated by the number of seed clams found each month. Figure 7 shows a time lag of about 2 months between the peak of the spawning season and the peak in the number of small clams.

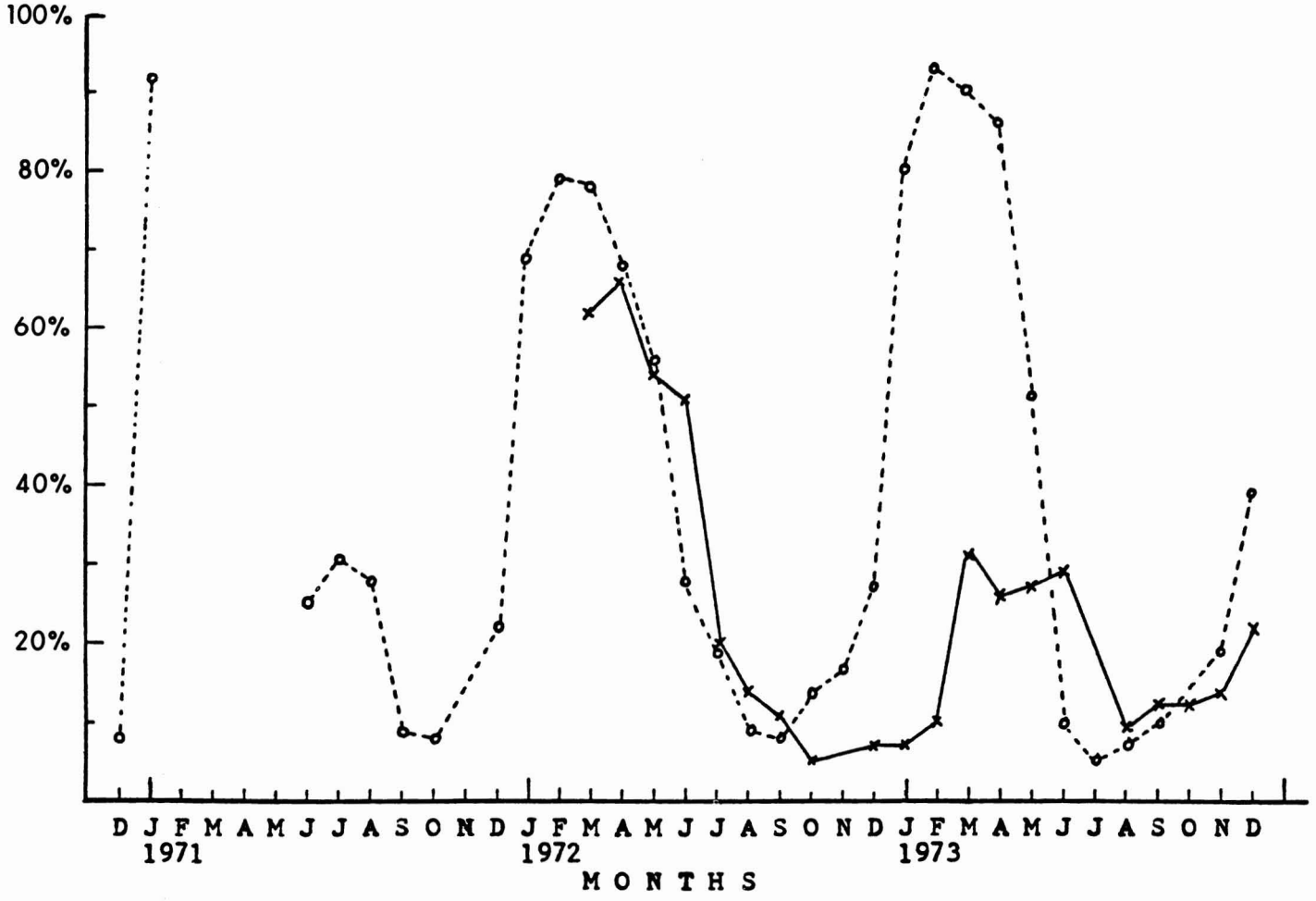


FIGURE 7. Monthly percentage of clams with flaccid gonads and percentage of juvenile clams in the monthly quantitative samples. Open circles, gonad condition; crosses, juvenile clams.

TABLE 6

CORRELATION BETWEEN THE NUMBER OF SEED CLAMS AND THE NUMBER OF LARGE CLAMS BASED UPON THE TOTAL POPULATION SURVEY OF MAY 1972

TRANSECT	CORRELATION COEFFICIENT AT TRANSECT		
	S versus L	M versus L	d.f.
A	0.084	0.484*	48
B	−0.011	0.082	48
C	0.265	−0.161	38
X	0.098	0.346*	68

NOTE: S, less than 5.5 mm; M, 5.5–11.4 mm; L, greater than 15.4 mm.
*Significant at $P = 0.01$ level.

distribution of the small clams is related to the distribution of large clams, a hypothesis which could be considered valid if significant correlation were found to exist between small and large clams. No such correlation was found in any of the transects. However, the number of intermediate clams was found to be correlated with the number of large clams in transects *A* and *X* (Table 6).

During the 4-year study period, an alternating pattern of good and bad years of recruitment was observed; there were many individuals below 15 mm only in the springs of 1970 and 1972 (Figure 8), although spawning was observed every year.

Settling

Higgins (1969) suggested that settling begins in February and ends in June with a peak in late April. My observations indicate that settling occurs throughout the year, with the peak occurring between April and May. Settling intensity is very low during other months of the year (Figure 7).

Many marine invertebrates are known to have some ability to select settling sites (Wilson 1932, 1937; Thorson 1957). To learn whether this was the case with *Tapes*, I grouped the clams collected during the May 1972 survey into three size-classes for each sampling point: small (< 5.5 mm), intermediate (5.5–11.4 mm), and large (> 15.4 mm). The number of small and intermediate clams were correlated with the number of large clams. I tested the hypothesis that the

Growth

I estimated growth rate by following the shifts in modes in the monthly length-frequency curves (Figure 8) after I separated the length-frequency into component normal curves using the probability paper method of Cassie (1954). The modes (Figure 9) were fitted to the von Bertalanffy growth curve using Fabens' (1965) computer program. (The original program which was in FORTRAN I was translated to BASIC.)

The von Bertalanffy growth parameter, k, was found to decrease with year (Table 7). I obtained the value of k from Higgins' 1968 data only after I considered the 4-year data together to obtain an average k. The estimate on the asymptote ranges from 50.70 mm (1973) to 46.74 mm (1970). The largest living clam found measured 48 mm, the largest

TABLE 7

PARAMETERS OF THE VON BERTALANFFY GROWTH CURVE, $L_t = L_\infty[1 - Be^{(-kt)}]$, AS OBTAINED FROM LENGTH-FREQUENCY CURVES OF NATURAL POPULATION AND EXPERIMENTAL DATA

	k (per day)	L_∞ (mm)	n
Modal progression			
March 1970–January 1971	0.003061	56.74	30
January 1971–January 1972	0.00246	52.57	27
January 1972–January 1973	0.00172	50.70	18
Combined, 1970–1973	0.00250	52.40	107
Higgins (1969)*	0.00246	63.00	—
Murphy (July–December 1970)†	0.00431	45.38	—

*Not given by Higgins in his thesis; calculated from average data given in the write-up.
†Experimental data; not conducted on study area.

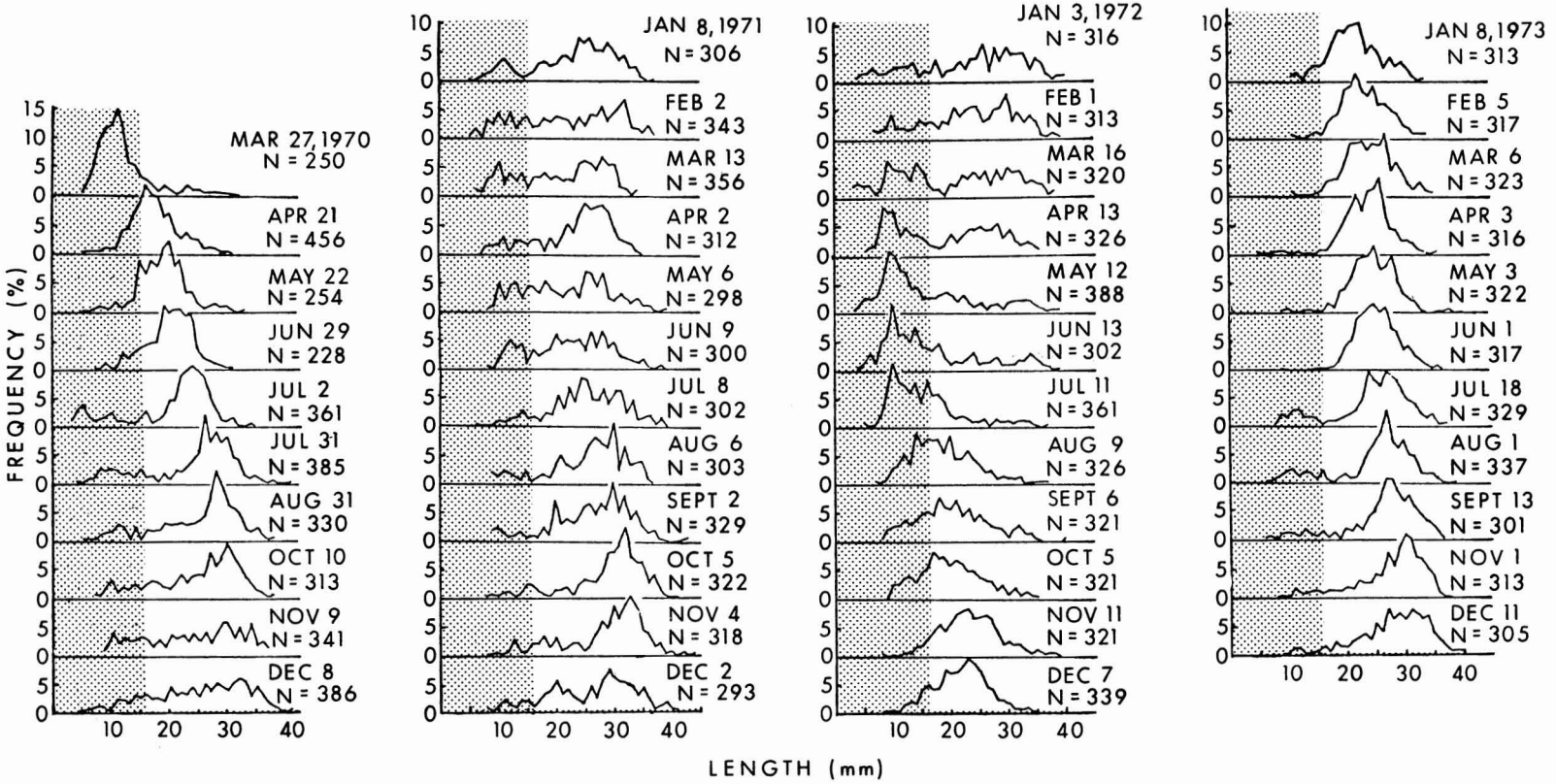


FIGURE 8. Monthly length-frequency distribution of *Tapes philippinarum*, March 1970 to December 1973.

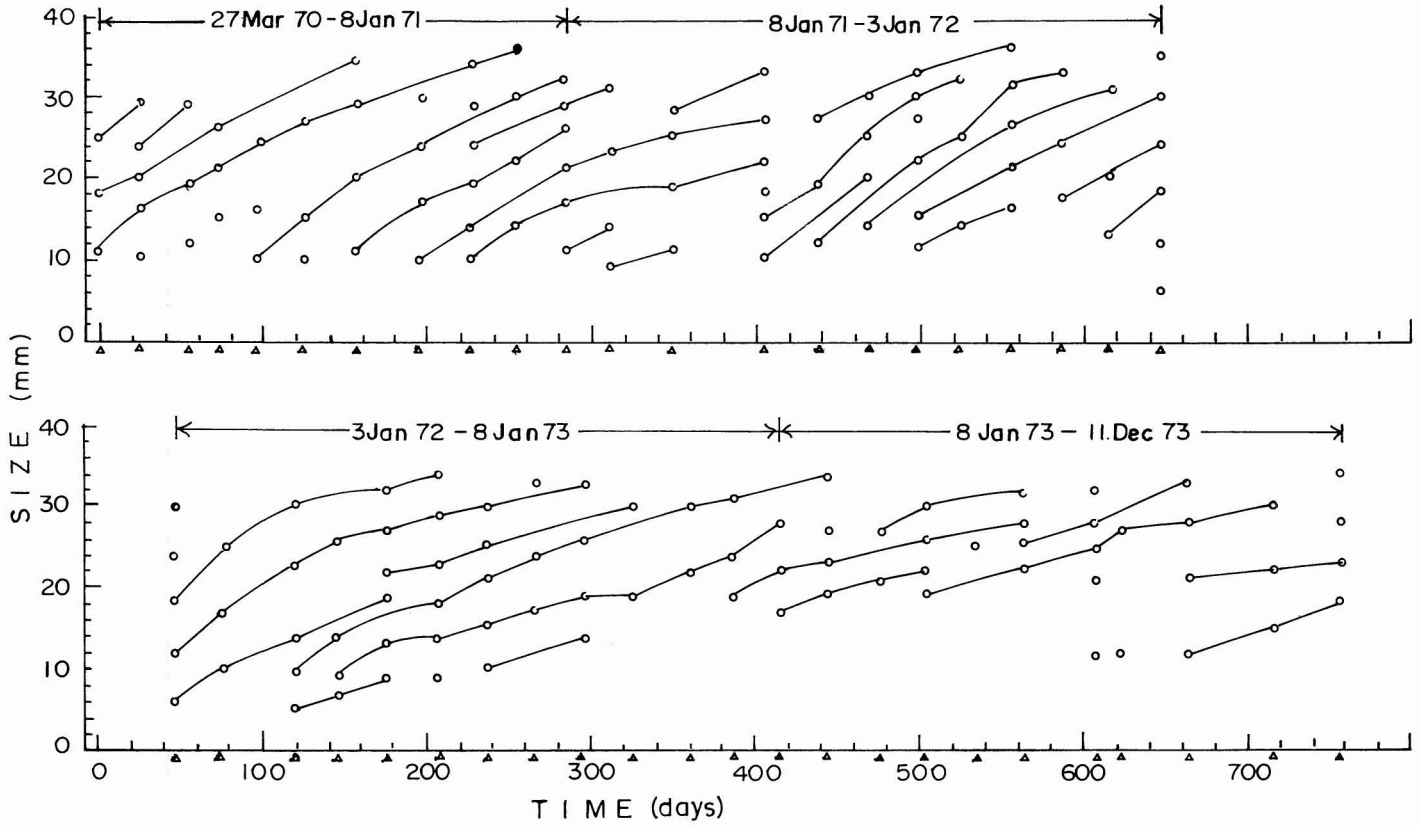


FIGURE 9. Progression of modes extracted from the monthly length-frequency distributions. The probability paper method has been used to separate the component normal curves from polymodal frequency distributions. Triangles along the curve indicate sampling days.

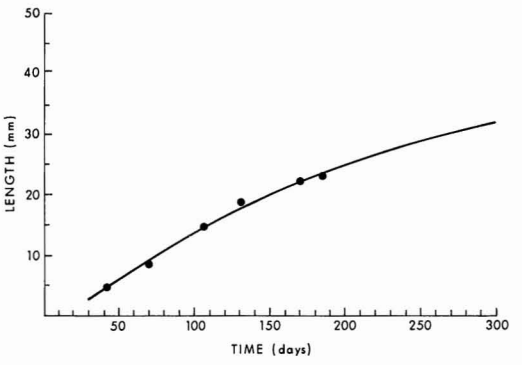


FIGURE 10. Growth curve for *Tapes philippinarum*. Experimental data from Murphy (unpublished).

empty shell, 52 mm. Few survive beyond 40 mm.

Experiments conducted by Murphy (unpublished), beginning with 5-mm clams, yielded a k of 0.00431, higher than the 0.00306 figures obtained from the modal progression of the natural population. However, the asymptote was lower than any obtained from the natural population (Figure 10).

Survivorship

The logarithm of the number of survivors (Table 8) plotted against age (Beverton and Holt 1957), gives a survivorship curve with a slope equal to $-z$, the instantaneous total mortality rate (Figure 11). If we use the least-squares regression, we get $z = 0.2005$, with the correlation coefficient $r = -0.95973$ with 24 d.f.

With the survivorship curve we can construct a life table to obtain a schedule of death. The only missing figure to make the life table complete is the number of clams at age zero, i.e., the number of clams at birth. We can obtain a reasonable approximation for the number of clams at birth per unit area by using the following data: (1) average density = 696/m² (obtained from May 1972 estimate of total population); (2) proportion

TABLE 8

NUMBER OF CLAMS PER 0.25 m² GROUPED BY AGE AT 2-MONTH INTERVALS; NUMBERS ARE BASED UPON DUPLICATE 225 cm² SAMPLES COLLECTED FROM FIVE STATIONS ALONG TRANSECT *A*, MARCH 1972 TO DECEMBER 1973; APRIL, MAY, AND JUNE COHORTS (UNDERLINED) ARE USED FOR ESTIMATING THE MORTALITY RATE

AGE GROUP (month)	SIZE RANGE (mm)	ODD MONTHS										
		Mar	May	Jul	Sept	Nov*	Jan	Mar	May	Jul*	Sept	Nov
2	<9.4	106	167	77	42		16	87	114		29	30
4	9.5–14.4	20	62	144	51		6	7	6		7	13
6	14.5–19.4	7	22	110	86		42	36	37		22	13
8	19.5–23.4	2	6	31	83		72	67	85		28	22
10	23.5–27.4	11	21	17	74		68	49	96		58	44
12	27.5–30.4	14	12	8	21		23	29	44		32	31
14	30.5–33.4	4	12	4	11		8	7	25		39	31
16	33.5–36.4	4	4	2	7		4	2	11		10	20
18	>36.5	3	4	1	3		0	0	6		8	11

AGE GROUP (month)	SIZE RANGE (mm)	EVEN MONTHS										
		Apr	Jun	Aug	Oct	Dec	Feb	Apr	Jun	Aug	Oct	Dec
2	<9.4	386	213	51	18	18	22	61	92	25	29	25
4	9.5–14.4	42	112	70	36	21	9	8	12	39	9	6
6	14.5–19.4	22	49	78	84	66	29	22	17	22	22	8
8	19.5–23.4	17	10	70	96	57	62	44	47	19	29	17
10	23.5–27.4	42	21	46	71	50	49	31	79	44	50	28
12	27.5–30.4	39	4	24	24	26	24	36	41	61	33	14
14	30.5–33.4	22	6	12	7	4	24	22	16	25	36	10
16	33.5–36.4	17	1	4	4	1	2	3	8	22	17	2
18	>36.5	0	3	3	0	2	0	6	1	6	7	1

*No sample collected.

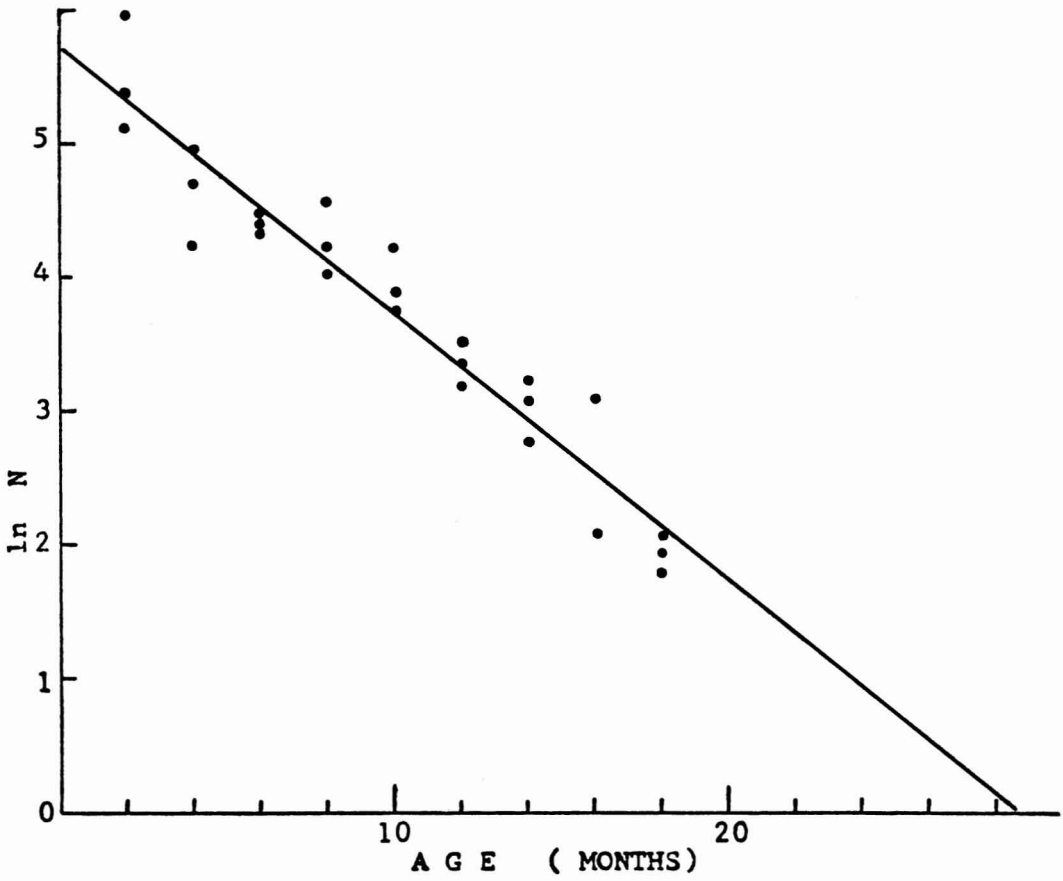


FIGURE 11. Survivorship curve, April, May, and June 1972 cohorts of *Tapes philippinarum*. The mortality rate, Z, is equal to the negative of the slope of the straight line; $Z = 0.2005$.

of clam population which potentially can breed—clams 20 mm and larger = 0.2056 (obtained from length-frequency from May 1972 total population survey); (3) sex ratio = 1:1 (obtained from monthly gonadal examinations); (4) proportion of spawners = 0.79 (obtained from percentage of clams with flaccid gonads in February 1972; see Figure 9); and (5) size-specific fecundity (refer to Figure 8).

With these data, we can calculate the density of female spawning clams as follows:

$$\text{Spawners/m}^2 = \frac{\text{average}}{\text{density}} \times \frac{\text{proportion}}{\text{females}} \times \frac{\text{proportion}}{\text{mature}} \times \frac{\text{proportion}}{\text{spawners}}$$

$$= 696 \times 0.5 \times 0.2056 \times 0.79$$

$$= 56.5 \text{ female spawners per m}^2.$$

We can calculate the average number of eggs all the spawners in a unit area potentially could produce by considering the size structure of the mature portion of the population and the size-specific fecundity. From the calculation in Table 9 an average of 1,137,000 eggs per spawner is obtained. If we assume that all the eggs were released at the same time, fertilized, and developed into larvae, then the number of larvae/m^2 = 56.5 spawners/m^2 × 1,137,000 eggs/spawner = 64.22 × 10^6. Since survivorship is expressed

TABLE 9

CALCULATION FOR THE EXPECTED TOTAL NUMBER OF EGGS RELEASED PER 100 SPAWNERS BASED UPON FECUNDITY AND LENGTH-FREQUENCY OF SPAWNERS

CLAM LENGTH (mm)	%, p	FECUNDITY, f (million eggs)	pf x 10^6
20	3.7	0.432	1.5984
21	3.6	0.492	1.7712
22	4.1	0.557	2.2837
23	5.3	0.628	3.3284
24	4.6	0.703	3.2338
25	4.9	0.784	3.8416
26	7.2	0.870	6.2640
27	9.1	0.962	8.7542
28	8.0	1.060	8.4800
29	10.5	1.163	12.2115
30	7.2	1.273	9.1656
31	8.8	1.388	12.2144
32	6.7	1.510	10.1170
33	5.2	1.639	8.5228
34	4.3	1.774	7.6282
35	3.5	1.916	6.7060
36	1.5	2.064	3.0960
37	1.1	2.219	2.4409
38	0.2	2.381	0.4762
39	0.2	2.551	0.5102
40	0.4	2.727	1.0908
			Σpf = 113.7349

in number per 0.25 m^2, then 64.22 $\times$ 10^6 divided by 4 = 16.05 $\times$ 10^6, the first entry in the life table (Table 10).

The life table presented is a schedule of death. Except for the number at age zero, which was independently estimated, the table is based upon the number of survivors in the April, May, and June 1972 cohorts.

Analysis of Empty Shells

One hundred sixty-seven empty shells collected over a 200 m^2 area on 5 February 1973 comprised the following categories: intact, 69; chipped or broken, 95; hole present, 3. The smallest empty shell found was 16.7 mm in length, the largest 45.4 mm. Using the same von Bertalanffy parameters that were used for the quantitative samples, I obtained the age-distribution from the size-frequency (Table 11). To find out if the age-distribution of the empty shells reflected and was correlated with the size-specific mortality rate obtained from the survivorship curve, I correlated the proportion of each age group to the total against column q_x in the life table (Table 10). The correlation coefficient of 0.94305 with 4 d.f. is significant at the 0.01 confidence level.

TABLE 10

LIFE TABLE FOR THE LITTLE-NECK CLAM, *Tapes philippinarum*, BASED UPON THE AVERAGE NUMBER OF SURVIVORS OF THE APRIL, MAY, AND JUNE 1972 COHORTS

AGE, x (month)	NUMBER OF CLAMS PER m^2	l_x	d_x	q_x	e_x
0	64 $\times$ 10^6	100 $\times$ 10^6	99,984,411	0.99998	0.5000
2	1,020	1,589	910	0.5727	2.0570
4	436	679	162	0.2386	3.1436
6	332	517	37	0.0716	2.9720
8	308	480	131	0.2729	2.1625
10	224	349	168	0.4814	1.7865
12	116	181	50	0.2762	1.9807
14	84	131	38	0.2901	1.5458
16	60	93	49	0.5269	0.9731
18	28	44	44	1.0000	0.5000
20	0	0	0	0	0

NOTE: l_x = number surviving at start of age interval x
d_x = number dying within age interval x to $x + 2$
q_x = rate of mortality
e_x = mean expectation of further life for animals alive at start of age x

TABLE 11

AGE-FREQUENCY ACCORDING TO CONDITION OF EMPTY SHELLS COLLECTED ON 5 FEBRUARY 1973; LIVE AGE-FREQUENCY AT THE SAME PERIOD IS INCLUDED FOR COMPARISON

AGE GROUP (month)	INTACT		CHIPPED OR BROKEN		PUNCTURED		TOTAL (%)	LIVE, >14.4 mm (%)
	Number	%	Number	%	Number	%		
6	6	3.6	2	1.2	1	0.6	5.4	13.1
8	12	7.2	18	10.8	2	1.2	19.2	38.5
10	15	9.0	21	12.6	—	—	21.6	29.5
12	8	4.8	17	10.2	—	—	15.0	12.2
14	11	6.6	14	8.4	—	—	15.0	3.8
16	10	6.0	10	6.0	—	—	12.0	2.6
18	7	5.2	13	7.8	—	—	13.0	0.3
Total	64	41.4	95	57.0	3	1.8	100.2	100.0

TABLE 12

CRAB CATCH USING TEN LIFT NETS SET 5 METERS APART WITH SHARK MEAT OR TUNA HEAD AS BAIT; APPROXIMATE DURATION OF EACH SET: 30–45 MINUTES

DATE		*T. crenata*	*T. integra*	*P. sanguinolentus*
11 November 1972	Number	17	6	2
	Size range (mm)	2.78–4.40	2.86–3.77	6.13–8.05
12 November 1973	Number	18	6	0
	Size range (mm)	2.90–4.50	2.70–3.60	—
18 November 1973	Number	20	5	1
	Size range (mm)	2.65–4.60	2.84–3.52	6.50

TABLE 13

PERCENTAGE OF CLAMS EATEN PER AGE GROUP BY *Thalamita crenata* IN 3 DAYS AND IN 8 DAYS; CRAB *A*: 51.5 mm, MALE; CRAB *B*: 65.2 mm, MALE; CRAB *C*: 45.8 mm, FEMALE

AGE GROUP OF CLAMS (months)	CRAB *A*			CRAB *B*			CRAB *C*		
	Initial number of clams	% eaten		Initial number of clams	% eaten		Initial number of clams	% eaten	
		3 days	8 days		3 days	8 days		3 days	8 days
2	4	0	0	5	0	0	5	0	0
4	6	67	67	5	0	0	17	24	29
6	18	89	94	17	24	47	10	20	20
8	17	88	94	20	30	45	8	0	12
10	15	80	100	13	46	46	5	0	0
12	8	25	75	9	22	56	5	0	0
14	6	17	17	6	0	0	0	0	0
16	6	0	17	5	20	20	0	0	0

TABLE 14

PERCENTAGE OF CLAMS EATEN PER AGE GROUP BY *Calappa calappa* IN 8 DAYS; CRAB *A*: 76.1 mm; CRAB *B*: 82.8 mm

AGE GROUP OF CLAMS (months)	CRAB *A*		CRAB *B*	
	Initial number of clams	% eaten, 8 days	Initial number of clams	% eaten, 8 days
2	7	0	1	0
4	13	15	9	44
6	13	62	16	6
8	7	43	14	0
10	12	50	13	8
12	8	38	11	9
14	10	40	6	0
16	5	20	5	0
Total	75	36	75	9

Predation by Crabs

Crab trapping on three different dates indicated *Thalamita crenata* to be the most abundant crab species on the clam bed, followed by *T. integra*, with *Portunus sanguinolentus* a poor third (Table 12). The box crab, *Calappa calappa*, was not caught by the nets used. Box crabs were rarely seen on the clam bed but appeared to be more abundant in the depleted beds.

Predation experiments using *Thalamita crenata* suggested a heavy predation pressure on clams within the 14.5 to 30.4 mm size range (Table 13). *Calappa calappa*, on the other hand, did not show any definite size preference (Table 14). The clams were grouped according to size groups equivalent to 2-month age intervals so that the results might be more easily compared with the other observations on mortality.

Clam density within the protected area did not differ much with that of the unprotected area: 36 clams were collected from a 25 × 25 cm quadrat from the unprotected area and 39 from the protected area. The size structure, however, was significantly different (Figure 12). More large clams were found in the protected area. The quadrat sample within the protected area also yielded 43 empty shells; only 3 were collected from the unprotected area.

DISCUSSION

The distribution of *Tapes philippinarum* within the existing clam bed appears to be restricted to the intertidal and shallow subtidal zones and to sediments characterized by high gravel and low mud content. Density is high at the edges of the bed. (In Figure 3 these are points 4 to 10 at transect *X*; all along transect *A*, and points beyond 90 at transect *B*.) These high-density areas were also characterized by a relatively more pebbly surface. Many clams were found attached by their byssus to pebbles.

The low salinity runoff from Kaneohe Stream has no drastic effect on the salinity of the bed as a whole or to the distribution of clams within the bed. On only one occasion, in November 1970, was a mass mortality of clams observed to follow a heavy rainfall. However, mortality did not occur in all parts of the bed; it was localized within a high area. Low salinity may not have been the cause of death. *Tapes philippinarum* is known to be extremely tolerant of salinity changes (Cahn 1951, Higgins 1969). A thick deposit of silt blanketed the gravel bed after the heavy rainfall. Concentrations of silt are known to reduce or to stop completely the filtration rate in bivalves, thus affecting their feeding and respiration (Loosanoff 1961).

Year-round spawning in *Tapes philip-*

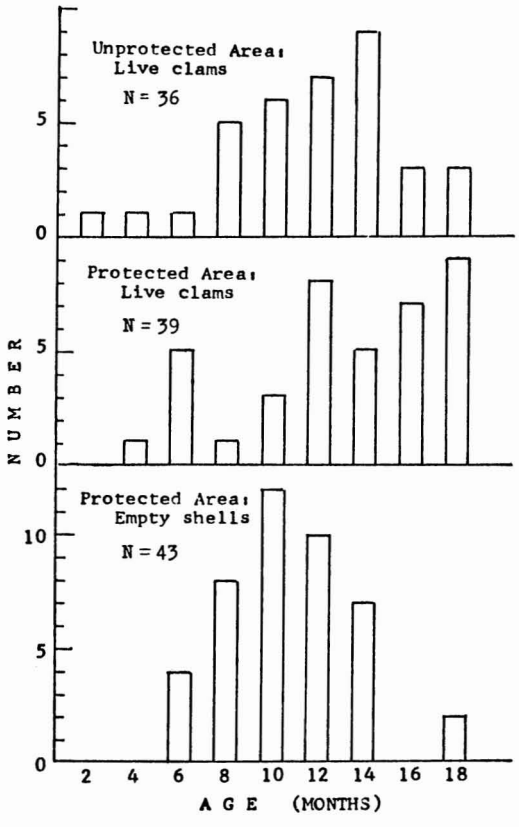


FIGURE 12. Comparative age-frequency of clams from control area and fenced area after 1 year.

pinarum is consistent with the bivalves' being in an environment where the seasons are indistinct. The peak in the spawning period from January to February was unexpected, however. The clams originally came from Japan, and spawning there differs from twice a year (April to June and October to December or March to April and August to December, depending upon the investigator cited) to once a year, late June to late August, in Hokkaido (Cahn 1951). An expected summer spawning was probably the rationale behind the setting by the Hawaii State Division of Fish and Game of the open season for clams from the first Saturday of December through the month of January.

Despite the clams' spawning each year, evidenced by the monthly gonad examinations, successful recruitment occurred only every other year during the 4-year study period. Thus, 1970 and 1972 were good years in terms of new recruits coming in, and 1971 and 1973 were poor years (Figures 3, 9). A similar observation was made by Hancock (1973) on cockles in Burry Inlet, South Wales: poor to moderate settlement in one year was followed by poor to exceptional settlement, and good to exceptional settlement was followed by poor to moderate settlement. Hancock demonstrated experimentally that the survival of settled cockle larvae is lower in patches of closely packed 1-year-olds than it is in patches of older and, therefore, larger clams, observations perhaps explained by less empty space between closely packed 1-year-olds than between older cockles or any other bivalves. Hancock suggested three mechanisms that might inhibit recruitment in closely packed 1-year-old bivalves: inhalation of newly settled clams by adult mollusks; entanglement of the spat in the pseudofeces produced by adults; and competition for space and food between the spat and adults.

The lack of correlation between the numbers of seed clams and large clams suggests that settling is random and is in no way related to the presence of large clams or to any specific area. The significant correlation between the intermediate-sized and large-sized clams was unforeseen. This observation suggests two a posteriori hypotheses which should be experimentally testable: (1) survival of settled clams is high in areas with high large clam density because of purely physical reasons such as substrate quality; and (2) survival of small, newly settled clams to intermediate size is enhanced by the presence of large clams.

It could be argued that the distribution of the seed clams is due purely to physical parameters such as scattering by wave action and not to the inability of the young organism to select settling sites. However, the distribution of the intermediate-sized clams within the high-density area is evidence against such an argument, as it is doubtful that the intermediate-sized clams are less likely to be scattered by wave action than the slightly smaller seed clams.

The empty shells provide a clue to the components of mortality. Intact shells would

be indicative of death by disease or parasitism, and chipped or broken valves, of crab predation. Shells also could have been broken by persons using a shovel or other digging instruments, but the level of illegal fishing was observed to be very low. Nor has fishing been observed within the sampling area. Holes were originally thought to indicate predation by gastropods. Because 95 of the 167 empty shells collected were broken, 57 percent of the natural adult mortality could be attributed to predation and the remainder to disease or parasites. Three shells with holes, making up 1 percent of the total, could not be attributed to gastropod predation, because the holes were not the small, neatly drilled holes characteristically produced by a snail's radula. They appeared, rather, to have been produced by birds such as the Ruddy Turnstone, *Arenaria interpres interpres* (Linnaeus), which is sometimes found within the intertidal area and which is known to include mollusks in its diet (Munro 1960). No signs of disease or large ectoparasites were noticed.

The significant correlation between the age-frequency of the empty shells and the size-specific mortality rate indicates that a systematic analysis of empty mollusk shells could be a useful tool in estimating mortality rates in this particular group of organisms.

The size-specificity of predation by *Thalamita crenata* is corroborated by the size distribution of chipped or broken shells. Broken shell size distribution indicates that the size range of predation in the clam bed is 19.5 to 30.4 mm; the size range was 14.5 to 30.4 mm in the predation experiment. The greater lower limit in the predation range as indicated by the broken shells can be attributed to a low number of clams within the 14.5 to 19.4 mm size range, which accounted for only 12 percent of the population at that time. In comparison, during the same month (February 1973), clams within the 19.5 to 24.4 mm size range comprised 37.23 percent of the population; 25.5 to 29.4 mm, 29.65 percent.

Unlike *Thalamita*, *Calappa calappa* did not exhibit a definite size-specificity. The two crab species approach their prey in different ways. *Calappa* was observed to get at the clam by chipping the valves little by little, starting from the tip. Higgins (1969) made a similar observation. *Thalamita*, on the other hand, uses its claw like a nutcracker. Chipping in the style of the *Calappa* would seem to be more size-independent than crushing in the style of the *Thalamita*.

Another difference between the feeding habits of the two species is worth noting, although it has no direct relevance to this study. Broken clam shells of *Calappa* were always found within that part of the experimental box where the clams were buried, but those of *Thalamita* were mostly scattered in small piles outside the substrate area. Thus, *Calappa* appears to consume the clam where it finds it, whereas *Thalamita* carries it elsewhere before feeding on it, the latter also being indicated by the presence of live, uneaten clams lying exposed outside the substrate area. Within the clam bed, *Thalamita* is often seen carrying whole clams.

Fencing effectively prevents crab predation. While the fencing experiment showed that the size structure of the fenced population is shifted toward larger sizes, it also showed that the density is not increased. The screen did not prevent settlement: all those clams less than 30.4 mm (1-year-olds) must have settled after the screen had been laid (the screen was laid in February and the peak in the appearance of seed clams in the substrate is from April to June). Nor did the screen prevent clams less than 11 mm from escaping, hence the absence of any empty small shells.

The absence of any difference in density between the fenced and unfenced areas could be interpreted to mean that any given area within the clam bed can support only a certain number of clams, beyond which later settlers would have little chance of surviving. Constant cropping by crabs in the unfenced area, on the other hand, may allow later settlers to survive, the number of survivors balancing the number lost through predation.

CONCLUSION

Total population estimates of 3.09×10^6 in 1970 and 3.40×10^6 in 1972 indicate that

the clam population in Kaneohe Bay increased at the rate of 1.1 clam per clam in 2 years or 5 percent per year. There appeared to be no further growth in 1973.

The rate of increase of the clam population is modest. Spot checks in the depleted beds revealed some signs of resettlement, although density in these areas is still very low.

Predation by crabs turns out to be a very important component in clam mortality. Fencing, although not shown to affect clam density, could be a useful technique to make more large clams available as breeders.

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